

STONES, CEMENT AND GUARDS IN HALICTINE NEST ARCHITECTURE AND DEFENSE

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ABSTRACT

Nest entrances of halictine bees provide an important interface between the outside world and the brood area, and they often show specific structural peculiarities. The openings serve constructional and nutritional functions, to which a defensive element is sometimes added in the social phase (supraorganism). The evolution of hidden and conspicuous nest entrances may regulate a density dependent mechanism for breeding populations of *Erylaeus malachurus*.

FUNCTION AND TYPES OF NEST ENTRANCE

Many aculeate hymenoptera nest in a variety of soils and construct one or several tunnels leading to a series of brood cells. Solitary species usually build less than twenty of these cells whereas a burrow of a social form contains many eggs and larvae during the summer. Such a potential source of high grade protein is exploited by diverse enemies which have often evolved ingenious methods to gain access to the buried treasures. The nest inhabitants are the first line of defense and must be eliminated before the nest is entered (Richards, 1965). The nest entrance therefore plays an important role not only in the removal of soil from the underground construction and in the passage of foragers but also as a distinctive landmark for the nest inhabitants and their parasites. Many halictine nests are built in aggregations, mainly because females establish new nests in the vicinity of existing ones. The range and diversity of nest entrances is striking in halictine bees and reflect the different behavior patterns and adaptations of the various species.

A hole in the ground is probably the simplest stage in the evolution of this structure. The expelled soil often forms temporary piles around the constricted entrances of *Halictus ligatus*, *Erylaeus malachurus*, *Dialictus imitatus*, *D. rohweri* and many more. *Halictus serripunctus* and *Dialictus zephyrus* have simple openings in vertical cliffs.

Several species excavate loose soil more frequently so that a tumulus is a constant feature around the nest entrance. This has been observed

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in *Lasioglossum leucozonium*, *E. nigripes* and *E. oenotherae*. The consolidation of the soil gives this structure a more lasting appearance in *H. quadricinctus* and *H. scabiosae* and also locates the nest entrance near the top of the cone. A progressively higher "chimney" indicates the age of the perennial *E. marginatus* nests (Plateaux-Quénu, 1959; Fig. 1). A further elaboration of turret construction is seen in *E. linearis*, *E. bimaculatus* and *Angochlorella striata* (Fig. 2).



FIGURES 1-3. FIG. 1. Two unguarded nest "chimneys" of *E. marginatus*; FIG. 2. Female of *E. bimaculatus* entering turreted nest with pollen; FIG. 3. Nest of *E. malachurus* showing closed entrance, surrounded by the cement-like tube; irregular hole indicates the activity of parasitoids.

Free-lying nests or those surrounded with tumuli and turrets give better landmarks to homing foragers but must also facilitate the growth of a resident parasite population, which finds no hardship in locating suitable host nests. It is not surprising that many halictine species habitually hide their nest entrances under stones, dead leaves or among vegetation. *H. patellatus*, *H. rubicundus* and *H. confusus* slant their nest openings in a way to make recognition from above more difficult. *E. cinctipes* is very adept in this technique by starting a vertical burrow with a normal entrance but slanting a secondary tunnel towards the surface while filling in the original opening. The top portion of the burrow is almost parallel with the soil surface for several centimeters before it is terminated under a stone or a clump of plants. Some of the turret-makers have similarly camouflaged their nest openings by curving the above-soil structure so that it points toward the soil surface rather than the sky (e.g., *E. interruptus*).

NEST CLOSURE

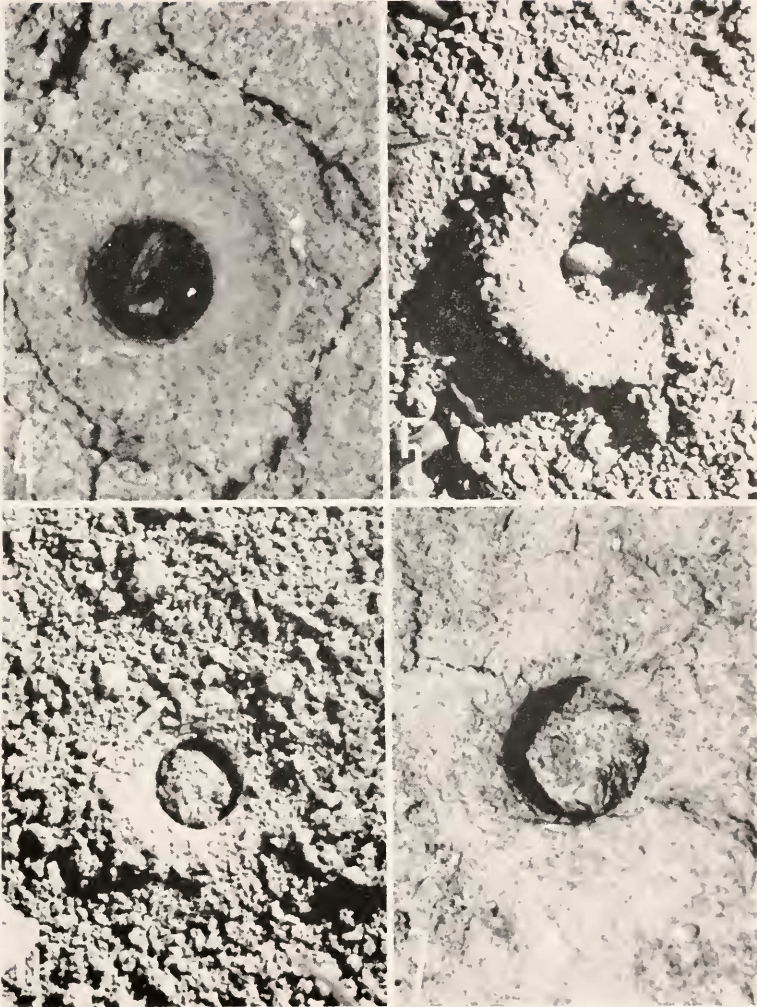
Almost all halictine bees close their nests during bad weather or at the end of a foraging period. The times at which the nests are sealed are different for the various species. The matinal *E. oenotherae*, for example, has most of the nests closed as early as 8.00 A.M., whereas *L. leucozonium* keep theirs open until around noon. Summer nests of the social species *H. ligatus* are rarely with a plug before 2.00 P.M. The halictines of hot climates have often two activity periods in the cooler parts of the day and close their nests after each session (e.g., *H. cochlearitarsis*, *H. holtzi* and *H. patellatus*). Nest closure and its element of camouflage seems to be effective against visual parasitoids as the cuckoo-bee *Sphcodes*, and the various flies of the genera *Bombylius*, *Leucophora* and *Glyphotriclis* but are less of a bonus against mutillid parasitoids. Females of the genus *Myrmilla* attack a great variety of halictine nests, but these are located by olfactory rather than visual cues.

The temporary sealing of nests after a day's foraging is not as elaborate as the closure at the end of a provisioning phase, especially in social species. There, a period of spring activity is separated from the matrifilial social phase in summer by several weeks of rest. The nests are deliberately closed before the inactive phase and plugs range from a few millimeters in *E. linearis* to 50 mm or more in *E. nigripes* and *E. cinctipes*. *E. malachurus*, which produces at least three distinct broods of workers during a Mediterranean summer, seals the nests after each provisioning phase; but the closures are progressively more imposing and range from 5 mm in April to over 200 mm in August.

Most of the closures are made with loose soil, brought up from the depth of the nest and pushed into place by the bee's abdomen. Several species seemed to have changed the type of plug and the way of procuring it. *E. nigripes*, for example, brushes loose soil particles into the burrow before pushing them into position in the entrance. A variety of Mediterranean forms have replaced the dry soil by more substantial material, especially stones. *H. cochlearitarsis*, *H. holtzi* and *E. pauxillus* were regularly observed to keep a fairly large stone at the bottom of the burrow, with which they plugged the entrance following periods of activity (Figs. 5, 6, 7). One female of *H. cochlearitarsis* used the same distinctive blue stone for five weeks, until the nest was excavated (Fig. 7). If the stone was pushed into the nest, the female would replace it within 20–30 seconds, rotating it for a perfect fit. All of the stones used were larger than the opening of the nest and could therefore not be removed without destroying the nest. Finally, the dimorphism of the nest closure of *H. maculatus* should be mentioned here. The overwintered females of this species close their nests with plugs of loose soil before the provisioning of cells has started. After that, a thin disc of moist soil, laid down in concentric rings is used for the nest closure, which blends very well into the surrounding soil.

NEST GUARDING

Architectural modifications are usually not effective in denying access to host-specific parasites and many industrious species protect their young by guarding the nest. The solitary *L. leucozonium* fiercely defends her nest against any intruders. Continued irritation is met by abdominal presentation and finally by nest closure. Blocking the nest opening with the abdomen is a common defensive pattern in many nearctic halictines (e.g., *H. ligatus*, *E. cinctipes*, *D. imitatus* and *D. rohaveri*), but is rare in paleartic species which keep their head in the entrance or present the nape (e.g., *E. malachurus*). The overwintered females of *H. scabiosae* and *E. malachurus* show agonistic behavior towards usurping conspecifics during the solitary spring phase (Knerer and Plateaux-Quénu, 1967). Continuous guarding is only possible when more than one female is in a nest, either in the pleometrotic spring associations or the matrilineal summer societies. Nonreproductive workers show often "altruistic" behavior when they sacrifice their lives in an attempt to save the attacked colony. However, guarding behavior appears scattered over many species without regard to their social status. *H. ligatus*, *H. cochlearitarsis*, *H. rubicundus*, *E. malachurus*, *E. pauxillus*, *D. imitatus* and *A. striata* have guarding of summer nests in common despite large differences in their levels of social



FIGURES 4-7. FIG. 4. A dead *malachurus* worker rests on top of the nest closure; the entrance is protected by the hard tubular structure; FIG. 5. Nest entrance of *H. holtzi* closed with one large and a few small stones; FIG. 6. Closed nest entrance of *E. pauxillus*; a single large stone is wedged into the constricted part of the burrow; FIG. 7. The "blue stone" of the *H. cochlearitarsis* nest observed for five weeks.

evolution. On the other hand, the advanced social *E. marginatus*, *E. linearis* and *E. nigripes* never guard the matrilineal nests although the pleometrotic nests of *E. linearis* are defended effectively.

NEST AGGREGATION AND POPULATION DYNAMICS

The trend towards hidden entrances is probably adaptive against parasitization by a wide variety of parasitoids. Specific parasitoids have to match every behavioral innovation of their hosts to remain successful. Bee nests are either located by following a pollen laden host to the nest (e.g., *Leucophora* and *Glyphotriclis*) or by searching suitable terrain systematically. *Sphccodes monilicornis* appears to do very well with the second method, although the females seem to miss the odd nest amongst vegetation. But many nests of *E. malachurus*, its main host, are placed conspicuously in large aggregations and are impossible to miss. This is an odd situation for an otherwise very adaptable and highly successful bee, and it seems paradoxical that this flippant behavior pattern can defy such intense evolutionary pressure. It can be argued, however, that camouflaged nests with their higher survival rate have become secondary in this species, and succumbed to more important mechanisms. There is a strong inference that the losses inflicted by the parasitoids can be made up quite easily, as a consideration of the species' bionomics indicates. *E. malachurus* raises 2 to 3 progressively more populous worker broods during the summer and a mature nest can produce over 100 future queens. This rate of growth is many times that of solitary and primitively social halictines and the problem of overpopulation and overexploitation of limited resources has replaced that of mere survival. Observations on *E. malachurus* in various parts of Europe and by different investigators have shown that breeding activity is limited to a certain portion of the female population, and this seems to be quite constant from one year to the next (Knerer, 1969). The "surplus" females were physiologically inhibited from starting nesting activities, probably by some visual cues emanating from the density of the aggregation; these potential queens died without leaving a progeny, unless they could usurp a nest which was already established. It seems clear that only well marked nests, visible to the whole population could meet the requirements for a density dependent mechanism, which would then explain the selective value of overly conspicuous nest entrances in *malachurus* and a few other common social species.

Appropriate defensive adjustments have seemingly been made to partly counteract the disadvantages of conspicuous nests. Guarding in this species reached a high level and it is not rare to see a small colony completely eradicated before the parasitoid can gain entry into the nest. By the same token, both *Sphccodes* and *Myrmilla* can gauge the strength of a colony and leave populous nests alone. The thorough nest closure after each provisioning phase reduces the vulnerability of the nests still further and a barrier of soil can be built up quickly even after the attack had begun. The success

of all defensive manoeuvres clearly depends on a unique structural feature of *malachurus* nests. It makes its appearance after the first worker brood emerged and consists of an extremely hard tube, 2 mm thick and 20 to 30 mm deep (Figs. 3, 4). It completely surrounds the entrance and protects the guards by its sheer hardness from the mandibles of the attackers. The ontogeny of the structure is not known but it is probably formed from a mixture of soil and saliva. Parasitoids are usually forced to excavate their own tunnels to bypass the cement tube or wait until rain renders the structure more soft and pliable (Fig. 3).

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